ASPECTS OF THE BIOLOGY AND SYSTEMATICS OF SOIL ARACHNIDS, PARTICULARLY SAPROPHAGOUS AND MYCOPHAGOUS MITES

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ABSTRACT

Among members of the class Arachnida, the saprophagous and mycophagous mites are the most diverse and abundant in soil systems, and have the greatest effects on soil structure and fertility. In most soils, the oribatid mites are the only arachnids which directly affect soil structure; they ingest particulate food and produce discrete fecal pellets, the possible functions of which are discussed. Current research is finding an active gut microflora in both saprophagous and mycophagous oribatid mites. For those species in which the diet varies seasonally, it is suggested that the gut microflora also changes, reflecting the new substrates. Particulate-mycophagy is a very old feeding habit, and was probably the ancestral one of the earliest known (Devonian) oribatid mites. Saprophagy may have originally developed as a mechanism for obtaining non-surface microbial tissue or exometabolites from decaying higher plant materials. The use of the plant structural parts as food may have been made possible by changes in gut microflora. The mite suborder Prostigmata also contains important soil mycophages, but these feed intracellularly and contribute little to soil structure. They are more "r-selected" than oribatid mites and may show numerical responses to temporary increases in food supply.

The descriptive taxonomy and systematics of North American saprophagous and mycophagous soil mites are in a poor state. Currently no "user-friendly" monographs are available for any major group, and higher classifications based on the methodology of phylogenetic systematics are only beginning to be proposed.

RÉSUMÉ

Parmi les membres de la classe des Arachnides qui vivent dans les sols, les mites saprophages et mycophages sont les plus divers et les plus abondants, et sont ceux dont les effets sur la structure et la fertilité des sols sont les plus marqués. Dans la plupart des sols, les mites oribatides sont les seuls arachnides qui affectent directement la structure du sol; elles ingèrent des aliments particulaires et excrètent des boulettes fécales, dont les fonctions possibles sont examinées. Les recherches actuelles révèlent une flore active du tube digestif chez les mites oribatides autant saprophages que mycophages. Chez les espèces dont la diète varie saisonnièrement, il est possible que la microflore du tube digestif change aussi, reflétant ainsi les divers substrats. La mycophagie particulaire est une très vieille habitude alimentaire qui remonte probablement aux plus anciennes mites oribatides connues (du Dévonien). La saprophagie pourrait à l'origine être apparue comme un mécanisme permettant d'obtenir des couches sous-jacentes de tissus microbiens ou des exométabolites provenant de plantes supérieures en décomposition. L'utilisation de parties structurales des plantes comme nourriture a pu être rendue possible par des changements dans la microflore du tube digestif. Les mites du sous-ordre Prostigmata incluent aussi d'importants mycophages du sol, mais ceux-ci se nourrissent intra-cellulairement et ne contribuent à peu près pas à la structure des sols. Elles sont davantage soumises à la r-sélection que les mites

oribatides et peuvent voir leur nombre augmenter à la suite d'un accroissement temporaire de la quantité de nourriture disponible.

La taxonomie descriptive et la systématique des mites nord-américaines saprophages et mycophages des sol est dans un état lamentable. Présentement il n'existe aucune monographie d'utilisation facile pour aucun des groupes majeurs, et des classifications supérieures basées sur les méthodes de la systématique phylogénétique commencent à peine à faire leur apparition.

INTRODUCTION

The subject of biology and systematics of the Class Arachnida is large even if one's attention is restricted to soil dwellers. Representatives of this class usually dominate the arthropod fauna of soils; numbers in the hundreds of thousands per surface m² are common (Petersen, 1981a). The soil arachnid fauna can be conceptualized and categorized from many viewpoints, but the one used here is that of function, particularly predation, saprophagy and mycophagy.

Predation is the most ancient and general feeding strategy of arachnids and predaceous species abound in soil and litter. Various groups of cursorial spiders constitute a major fraction of the larger (length > 1 cm) predaceous soil arthropods; pseudoscorpions and harvestmen, along with other spider groups, are intermediate (1 mm - 1 cm) in size. By far the greatest diversity of small arthropod predators in most soil systems is contributed by representatives of two suborders of mites, the Mesostigmata (temperate region soil dwellers are mostly predators) and the Prostigmata (in part). The latter group also includes taxa which are external parasites of other arthropods. Little will be said here regarding these predators and parasites, since their influence on physical and chemical attributes of soil is at best indirect, through their regulatory interactions with other soil animals. This is not meant to infer that they are unimportant to the proper functioning of soil systems; we simply have little empirical information. Progress has been made in understanding the role of spider predation in agroecosystems (Riechert, 1984), where they are generalist background regulators of insect populations, but their role in soil/litter systems is virtually untested, except for the work of Clarke and Grant (1968) and Kajak and Jakubczyk (1977), who demonstrated higher densities of centipedes and saprophages such as collembolans after removal or exclusion of spiders and other large predators. Even the detailed study by Moulder and Reichle (1972) on the significance of spider predation in the forest floor fell short due to lack of information on prey dynamics. The role of predation in regulating soil arthropod and nematode (see Karg, 1983) densities remains, for the most part, unknown. An exception is the important role of predaceous Tydeidae (Prostigmata) in regulating bacteriophagous nematode populations in desert soils (*e.g.,*, Whitford and Santos, 1980).

It is the arachnid groups generally considered to be saprophagous and mycophagous (fungivorous) which are of greatest interest from the standpoint of soil structure and fertility, and these will be stressed in the discussions which follow. Saprophages, those feeding directly on decomposing leafy or woody vegetation (macrophytophages of Schuster, 1956) have the greater significance in producing structure in organic horizons, particularly by comminution activities and production of feces. Among the Arachnida, mites of the suborder Oribatida (Cryptostigmata) perform this function on a scale which is small in size, but not necessarily in overall effect. Fungivorous mites abound in soils, and along with Collembola form the dominant mycophages in most terrestrial ecosystems (Seastedt, 1984). Two general fungal-feeding strategies are apparent: the fungivorous oribatid mites are particulate feeders, and produce discrete fecal pellets which contribute to soil structure. The fungivorous prostigmatid (trombidiform) mites feed intracellularly by means of stylettiform chelicerae and contribute

little to soil fabric.

Due to the scope of the topic, available, this paper cannot be considered a complete review of current problems in arachnid biology and systematics. Only saprophagous and microphytophagous (bacterial and fungal feeders) arachnids will be dealt with in any detail. In particular, the oribatid mites are emphasized, for several reasons: 1) they are usually the dominant arachnid group in terms of numbers and biomass (Petersen, 1982a, 1982b); 2) they are apparently the most important group of soil arachnids from the standpoint of direct and indirect effects on the formation and maintenance of soil strucure; 3) they are the best known biologically, even if "best" is not very good; and 4) they are the soil animals with which I am most familiar. Little will be said of the mite suborder Astigmata; their occurrence in soils is sporadic and their overall importance is likely to slight (Luxton, 1981a; see O'Connor, 1982 and Woodring, 1963). Even with these restrictions my comments will be selective. From the standpoint of biology, I will deal particularly with certain aspects of nutrition, followed by brief remarks on population dynamics, and then review how the feeding activity of these animals affects soil structure and fertility. Lastly, I will offer some comments on systematics of soil arachnids, again with emphasis on non-predators.

BIOLOGY

Some Aspects of Oribatid Mite Nutrition

The diet and method of feeding of saprophagous and mycophagous soil mites greatly influences the effect they have on soil structure and fertility. Such information was rather scattered and anecdotal before Schuster's (1956) classic paper, which described feeding habits of a wide variety of European oribatid mite. Since that time numerous authors have approached the subject, generally using one or more of three methods: laboratory food preference tests, gut content analysis of field-collected specimens, or the study of gut enzyme complements [see studies and reviews by Wallwork (1967), Lebrun (1971), Luxton (1972), Pande and Berthet (1973), Behan and Hill (1978), Behan-Pelletier and Hill (1983), and especially Harding and Stuttard(1974)].

Each of these techniques has associated problems. Laboratory preference tests are limited by our ability to discern and supply the food items available in nature and to keep other, often unknown, variables within preference, or at least tolerance, ranges of the mites being tested. Simple choice experiments rarely fail to demonstrate preferences, yet these preferred foods may not, in some circumstances, be the ones chosen in nature, even if they are available (Mitchell and Parkinson, 1976). Also, even heavy feeding on a given food does not mean that reproductive or developmental success is necessarily possible (Luxton, 1972; Saichuae et al., 1972; Mitchell and Parkinson, 1976; Stefaniak and Senniczak, 1981).

Gut content analyses have the disadvantage that less easily digestible materials will be overestimated in dietary quantification (Behan-Pelletier and Hill, 1983). In some situations, readily digestible materials may be supplying most of an animal's requirements, yet rarely be seen in the gut by conventional methods. For example, it is unknown to what extent oribatid mites are predatory or necrophagous. Muraoka and Ishibashi (1976) and Rockett (1980) have demonstrated active feeding on living and dead nematodes by brachypyline oribatid mites and the importance of this in nature needs investigation. Stefaniak and Seniczak (1981) found that cannibalism could occur in oribatid mites in association with poor nutrition, and Behan-Pelletier and Hill (1983) found unusually high quantities of small animal remains in guts of acid-bog dwelling oribatid mites. They also suggested that the presence of such dietary

components might be related to the overall poor nutrient content of other available foods. The role of bacteria or other Monera, scraped from soil substrates, as food for oribatid mites is virtually unknown. Luxton (1972) demonstrated attractiveness of bacteria to some species, and Behan-Pelletier and Hill (1983) found high percentages of Monera in some oribatid guts, but whether they are truly food sources, or function as symbiotic sources of enzymes necessary to complement the mites' endogenous enzyme system, or both, remains to be elucidated (see below).

Studies of gut enzymes (Luxton, 1972; Zinkler, 1971, 1972) have been enlightening, but they are typically done on whole-body homogenates and give no information on the origin of any given enzyme. Luxton (1972, 1979) suggested that enzyme complements of oribatid mites correspond to the exhibited feeding habits. Species which are principally saprophagous (in particular the *xylophagous*, family Phthiracaridae) possess enzymes capable of hydrolyzing structural carbohydrates of higher plants (*e.g.,* cellulase, xylanase, pectinase), whereas those ingesting primarily fungal tissue can hydrolyze the fungal storage sugar trehalose and perhaps chitin, which is found in hyphal walls. Only panphytophagous (unspecialized) species possess both enzyme systems. Two other authors (Zinkler, 1972; Dinsdale, 1974), however, failed to find a cellulase in phthiracarid mites. There is mounting evidence that many carbohydase enzymes, including cellulase and chitinase, are produced by a diverse and very active microflora (Seniczak and Stefaniak, 1978; Stefaniak and Seniczak, 1976, 1981). These studies indicate that the composition of the gut microflora in both panphytophages and mycophages (and the enzymes produced) depends on the food ingested, and is not identical to the microflora of the surrounding environment. Their floral lists indicate that a subtraction process occurs. Those microorganisms capable of continued (or enhanced?) enzymatic production in the gut may be those which are resistant to digestion. Dinsdale (1974) has demonstrated that in *Phthiracarus* sp. (which had few demonstrated gut microflora) enzymes acting on the glucosidic bonds of simple storage carbohydrates were closely associated with the gut mucosa, and protein digestion appeared to be intracellular, with evidence of pinocytosis. One can speculate that these enzymes are endogenous, and that all enzymes acting on structural polysaccharides which are found in oribatid mite guts are of microbial origin, as they apparently are in all other arthropods which possess them.

It has been known for many years that saprophagous oribatid mites will only eat material if it has been previously attacked by microorganisms (see Harding and Stuttard, 1974), but the earlier consensus view was that the microbial tissue itself, or exometabolites from its decomposition activities, provided the only energy source. The finding of active gut microflora in saprophagous groups is not surprising, but it is somewhat surprising that fungivorous mites may have a strong dependence on gut microflora.

The implications and questions raised by Stefaniak and Seniczak's work are important ones and relate to the ability of soil mites to adjust to forced or opportunistic changes in diet. There is growing evidence (*e.g.,* Anderson, 1975; Swift, Heal and Anderson, 1979) that in some soils many or most oribatid mites do not adhere strictly to saprophagy or mycophagy throughout the year. Feeding is catholic, and gut contents of a given species can vary with site and season. At times even those species normally associated with strict xylophagy (Phthiracaridae) can be fungivorous, and those with chelicerae seemingly specialized for mycophagy, such as *Eupelops*, can be saprophagous (Wallwork, 1967; Anderson, 1975; Behan-Pelletier and Hill, 1983). Anderson (1975), working in a British deciduous forest, considered mycophagy to be the dominant feeding activity by oribatid mites soon after leaf fall in autumn. Within a rapidly

degraded litter layer, fungi were less easily available during the following season, and feeding activity changed to mixed mycophagy/saprophagy and then to saprophagy prior to the following leaf-fall. Such patterns were apparent even within populations of a given species.

A seemingly conflicting pattern was found, however, in a Canadian aspen forest soil (Mitchell and Parkinson, 1976) where the litter layer was more stable. The dominant taxa were primarily fungivorous and there were one or two seasonal peaks in feeding rate related to leaf-fall. Perhaps most interesting was the fact that overall feeding rate was related to general microbial activity, and opportunistic switiching to saprophagy apparently did not occur at this site. Nor did Behan-Pelletier and Hill (1983) find seasonal patterns in diet composition during a six-month study of feeding by oribatid mites in an Irish acid peat bog, other than opportunistic use of pollen. For the most part, species were panphytophagous. It seems that the existence of seasonal patterns in oribatid mite feeding depends on site characteristics, especially the rate of early decomposition. Where major diet changes do occur, as in Anderson's (1975) site, one can speculate that they are made possible by passive access to a rich variety of symbiotic microflora ingested with the food. Different bacterial floras (and their respective enzyme complements) may preferentially develop in the gut during the part of the season when the appropriate food enters the diet. Stefaniak and Seniczak (1976, 1981) have demonstrated such a relationship between food type and the composition of the gut microflora under both saprophagous and mycophagous feeding regimes. Perhaps in less active sites, such as that studied by Mitchell, changes in available microflora are insufficient to necessitate a switch, or perhaps climatic or other factors intervene when fungal availability is low, resulting in lower ingestion rates rather than dietary changes. The ability of any oribatid mites to change diet has been suggested to be adaptive from the standpoint of increasing survival probability in variable or different environments (Wallwork, 1958; Luxton, 1972), but it is interesting that the two most widely distributed (both geographically and ecologically) and successful species known, *Tectocepheus velatus* (Michael) and *Oppiella nova* (Oudemans), are apparently strictly mycophagous.

Saprophagy and Mycophagy in Other Soil Mite Groups

Compared to oribatid mites, little is known of the feeding biology of other mycophagous or saprophagous mite taxa. Members of the Uropodina (belonging to the predominantly predaceous suborder Mesostigmata) exhibit these feeding habits, (Krantz, 1978), but they do not constitute an important fraction of the soil fauna in most areas of North America; in the tropics they are much more abundant, often outnumbering oribatid mites. Like their predaceous relatives, they are predominantly liquid-feeders (Karg, 1963; Ahtias-Binche, 1977, 1981) so their influence on soil structure is probably minimal.

A different type of mycophagy is exhibited by some members of the suborder Prostigmata. The apparent majority of fungal-feeding soil Prostigmata to the families Eupodidae, Tydeidae, Tarsonemidae, Scutacaridae, and Phgmephoridae (Evans *et al.*, 1961; Karg, 1963; Krantz and Lindquist, 1979; Kethley, in press). Although present in soils of most ecosystems, these mites are especially abundant and diverse in herbaceous systems (where oribatid mites are usually not dominant) such as prairies, oil-fields and arctic sites (Petersen, 1982a) and also in desert soils (Santos *et al.*, 1978). In a study of an oil-field soil in Ohio (D. Dindal and R. Norton, unpublished) representatives of more than 100 species of Prostigmata were collected over several years, most belonging to the aforementioned families. Although there is little supporting information, their intracellular style of feeding would seem to preclude any direct impact on

soil structure, in contrast to the comminution and fecal production exhibited by particulate-feeding oribatid mites. They are not, therefore, strictly ecological equivalents, despite a common general food source. As with oribatid mites, mycophagous Prostigmata may demonstrate feeding preferences in laboratory tests (*e.g.,* Kosir, 1975). As might be expected, no active gut microflora has been reported from these mites. Fungivory is also known in another group of mites commonly associated with the Prostigmata, a group often referred to as the "Endeostigmata" or Pachygnathoidea. At least some members of this group are considered early-derivatives of the lineage which gave rise to oribatid mites (*e.g.,* O'Connor, 1984). Thus, it is not surprising to find particulate-mycophagy in some of these taxa, such as *Terpnacarus* (Theron, 1979) and *Grandjeanicus* (personal observation). This brings up the question of the evolutionary development of the various feeding strategies discussed to this point.

Comments on the Evolution of Mycophagy and Saprophagy in Acariform Mites

Intimate asssociations of arachnids and soils are as old as soils themselves (Kevan *et al.,* 1975). When terrestrial vegetation first began to flourish in Devonian times soil mites were already present, and in forms not very different from some which exist today. It is fortunate that some representatives of these ancient lineages have survived, because they give insight into not only the systematic relationships of early soil mites, but also their possible feeding habits. The earliest of the mite fossils, *Protacarus crani* from the Devonian Old Red Sandstone formation of Scotland (Hirst, 1923), is very similar to extant members of the "Endeostigmata" (Krantz, 1978), a loosely defined group which is currently thought by some (including myself) to have given rise independently to both the Prostigmata and the Oribatida-Astigmata lineages. Some extant members of the group are particulate-mycophages, as noted above. These have modified mouthparts with specialized setae (rutella) used in conjunction with the chelicerae to shear off particles as food is pulled toward the mouth (Grandjean, 1957; Theron, 1979), and appear to be part of the lineage which includes oribatid mites (also with rutella). Other "Endeostigmata," lack rutella (a few of these possibly secondarily so) and feed on spores or pierce roots to obtain nourishment (Theron, 1979). Although the mouthparts of *Protacarus* are not well described, they appear to be rather stylettiform and if so, are consistent with this feeding type. The earliest known fossil oribatid mite, also of Devonian age, is apparently a member of the extant family Ctenacaridae (Shear *et al.,* 1984) which are particulate-mycophages (Grandjean, 1954; personal observation). In none of these early derivative groups (fossil or extant) is there any evidence of saprophagy, which makes Krantz and Lindquist's (1979) suggestion, that mycophagy in oribatid mites evolved from saprophagy, difficult to accept. It is far more likely that sarcoptiform mites (those with a cutting rutellum) were ancestrally mycophagous, and fed on the rich terrestrial microflora which probably existed in the primordial organic soils developing concurrently with the growth and decomposition of the earliest vascular plants.

Saprophagy was apparently derived within the oribatid mites, seemingly associated with even stronger, more robust development of the rutellum and sclerotization in general. It is reasonable to speculate that the appearance of saprophagy gave previously mycophagous mites a mechanism for ingesting non-surface microbial tissue (or easily utilized exometabolites). The use of the higher plant structural material itself, by means of a symbiotic gut microflora derived from environmental sources, may have evolved later and perhaps necessitated changes in gut chemistry to allow or promote the growth of gut bacteria and actinomycetes.

In any event, it is clear that mycophagous and saprophagous soil arachnids were not added to soils as an evolutionary "after thought", except perhaps some of the intracellular-mycophagous Prostigmata (see Krantz and Lindquist, 1979). Rather, the soil system as we know it today, with its complex patterns of energy flow and nutrient cycling, is a result of a coevolution between mites and other soil animals (the ecologically similar Collembola are equally as old), the microflora, and the developing terrestrial vegetation.

A Brief Overview of Development and Population Dynamics

Knowledge of developmental biology and population dynamics of saprophagous and mycophagous mites is essential for determining the magnitude of their relationship to soil structure and fertility. Here again, we know much more about oribatid mites than the mycophagous taxa of Prostigmata. Early estimates of developmental times for oribatids are mostly useless, since they were done with laboratory cultures at high, constant temperatures (20–30° C) and with constantly high humidity and food supply (see Lebrun, 1971; Luxton, 1981b for reviews). Consequently, grossly underestimated development and generation times were the rule. Multivoltine life histories were commonly suggested for temperate-zone oribatid mites despite the fact that annual mean temperatures in in the soil may be only half those of the laboratory. The complexity and variation of natural abiotic and biotic factors make simple extrapolations impossible, in light of our knowledge of such factors as high development Q_{10} values (Lebrun and Ruymbeke, 1971), variable temperatures (Lebrun, 1977), and food quality (Saichuae *et al.*, 1972; Mitchell and Parkinson, 1976; Young and Block, 1980; Stefaniak and Seniczak, 1981) upon developmental time, survival rates, and metabolic rates of these mites.

Improved estimates have resulted from following population age-structure in the field over time (*e.g.,* Mitchell, 1977; Thomas, 1979; Luxton, 1981b, 1981c). There are difficulties with this method, however, when oviposition is not temporally circumscribed. Also, some workers have equated developmental time (egg-adult) with the more ecologically significant generation time (adult-adult). For example, Weigmann's (1979) estimate of a one-year generation time in *Platynothrus poltifer* (Koch) is possible only if eggs are laid immediately after the adult instar is reached. As Harding (1973) has shown, however, a long preoviposition period is typical for this species and what Weigmann probably observed was two principal cohorts in a population with a one year development time, but a nearly two year generation time.

The recognition of preoviposition periods and the possible presence of cohort structure suggests a need for reexamination of earlier age-structure data. It is likely that natural developmental times of oribatid mites in temperate regions (where they are generally most abundant) take a year or more, and two-year generation times are probably not uncommon. Longevity is probably relatively high in natural conditions, with iteroparity common (Mitchell, 1977; Luxton, 1981b); this may keep cohort recognition from being absolute.

Mortality factors in oribatid mite populations are poorly known. Lebrun (1969) and Mitchell (1977) suggested that mortality is concentrated in the immatures; presumably this is mostly due to predation on these soft-bodied instars and the rigors of the molting process. But adults are not immune to predation (Riha, 1951; Norton and MacNamara, 1976) and they seem to be more vulnerable to internal parasaites (*e.g.,* Purrini, 1983 and included references). Cold-induced winter mortality may not be important (Mitchell, 1977). Adaptations to survive subfreezing temperatures have been elucidated (*e.g.,* Somme and Conradi-Larsen, 1977; Block, 1980) and include elevation of cryoprotectants (such as glycerol) in the hemolymph and the cessation of feeding to avoid the presence of ice nucleating agents in the gut. Feeding activity

during subfreezing winter temperatures may require the surpassing of a snow-thickness threshold (Aitchison, 1979).

Oribatid mites can generally be considered K-selected organisms (Mitchell, 1977). Their high diversity, low fecundity (*e.g.,* Luxton, 1981b), increased variability in instar length as development procedes (Lebrun, 1971; Luxton, 1981b), and high longevity coupled with iteroparity, create an overall relatively stable community, especially in forest soils. The higher oribatid mite densitites often noted during winter (see Harding and Stuttard, 1974) may be artifacts of the sampling process in two different ways. Persson and Lohm (1977) found that soil compaction during sampling trapped significant numbers of microarthropods, except when the soil was frozen. Also, as reviewed by Luxton (1981b), about one-third of an oribatid mite's post-hatching development time is spent in pre-ecdysial resting stages and Lebrun (1969) has noted that this can cause substantial under-estimates of population densities calculated from desiccating-style extractors. Since molting occurs primarily during warmer months, under-estimation should especially be a problem in this period. It may be that in temperate regions the best overall estimates of population density are those obtained in late fall or early winter.

Information on population dynamics of mycophagous Prostigmata (*e.g.,* Heterostigmata, Tydeidae, Eupodidae) is much less extensive. Information about structure of age-classes is almost non-existent, but multiple generations per year seem to be likely (Luxton, 1981d). Unlike oribatid mites, they may show numerical responses to temporary increases in food supply. Very high densities are commonly found in litter-bag studies (Crossley and Hoglund, 1962; personal observations), where the compact, moist substrate is conducive to rapid mycelial growth. At least some of these taxa (although certainly not the "Endeostigmata") are r-selected as is apparently so for some of their phytophagous aerial relatives (Krantz and Lindquist, 1979).

The Role of Saprophagous and Mycophagous Mites

The literature on the role of saprophagous and mycophagous mites and collembolans in the functioning of soil systems is full of contradictions (Cancela de Fonseca and Poinsot-Balaguer, 1983), especially from the standpoint of whether or not their activities are necessary for expeditious decomposition of annual organic matter input. What is now clear is that these animals, even when abundant, use a very small amount of the annual energy input to the soil-litter system, generally less than 1% (Mitchell, 1979. Thomas, 1979; Luxton 1982a). This is principally due to their small standing crop biomass combined with a low weight-specific respiratory metabolism (Mitchell, 1979). Even in the absence of significant direct use of energy, the modern consensus is that they "earn their keep" indirectly through comminution and relationships with soil microflora. In reviewing standardized results of exclusion experiments, Seastedt (1984) calculated an average contribution by microarthropods of 23% to reduction of standing litter crop. Much research has gone into explaining results from these "black box" experiments, reviewed most recently by Seastedt (1984).

Saprophagous and mycophagous mites, particularly oribatids, influence soil structure by comminution of organic inputs, the production of fecal pellets and perhaps the prevention of fungal matting. Burrowing activity is limited to internal tissues of leaves, petioles, twigs, etc. and mineral particles are rarely ingested, or at least rarely reported (Harding and Stuttard, 1974). The only clear instance of organic-inorganic soil mixing by a mite seems to be that reported by Robaux *et al.* (1977), who, under laboratory conditions, found that *Tyrophagous*

putrescentiae can create mixed microaggregates in clay soil and increase aeration by the formation of cavities. Direct vertical and lateral translocations of organic matter are probably insignificant, since soil mites are rather sedentary on a diurnal basis and generally defecate on or near their food source. The significance of fecal pellet production by soil mites and collembolans is usually considered to be the increased surface area (relative to uncomminuted material), increased water-absorbing qualities, higher nitrogen concentration, higher pH and their small size, which allows illuviation into lower soil horizons. All these actions purportedly increase microbial activity, especially that of bacteria, as bacterial populations flourish in the higher pH regimes of the gut, feces and lower horizons. Since bacterial activity is a surface phenomenon, constantly requiring fresh surfaces (Luxton, 1981e) the comminution aspect seems especially important. When feeding occurs on leaf mesophyll, for example, not only is new surface exposed, but the food particle itself is subjected to decomposition in the gut and in the fecal pellet eventually formed. Increases in surface area due to fecal pellet formation are modest, however. Nef (fide Harding and Stuttard, 1974) found a 10,000-fold increase in surface area of a conifer needle when comminuted by a phthiracarid mite, but reformation into pellets reduced this to a 4-fold increase.

Although fecal pellets may decompose readily in certain situations (*e.g.,* Jongerius, 1963), especially when moved downward in the profile, they are often rather long-lived (Grosbard, 1969; Webb, 1977; Bal, 1982) and accumulate, especially in mor soils with few large invertebrates to actively mix materials. Webb (1977) has noted that high cohesive forces between pellet particles, especially very small ones, are apparently the cause of this general recalcitrance, which is not observed with feces of larger arthropods. The most important function of small fecal pellets may be that they maintain the highest possible surface area for decomposition. He suggested there is a theoretical lower limit to size of free particles in the soil, and if not compacted into pellets the bite-sized particles would form even larger aggregates. Other work suggests that the increased surface area of mite fecal pellets is ineffective in increasing decomposition of the contained material. For example, the decaying grasses studied by Grosbard (1969) showed rapid decomposition after being fed upon by mites, but the fecal pellets decomposed very slowly. Perhaps mite feeding has an ecological cost associated with it, especially in the absence of soil mixing, or the slower decomposition of feces may serve an important regulatory function in some situations. The overall impact of comminution by saprophagous mites on soil structure and decomposition depends to some extent on the proportion of annual organic input which they ingest. Recent studies (Mitchell, 1979; Thomas, 1979; Luxton, 1981e) suggest that the figure may be almost insignificant (less than 2%) although few soil types have been studied. However, a small amount of feeding may go a long ways toward opening up new substrates for microbial decomposition. Equating mite ingestion rates with their contribution to decomposition processes maybe as fallacious as equating the metabolic contributions of soil animals to their importance in soil systems.

For two decades the concensus has been that the real importance of saprophagous and mycophagous mites and other microarthropods has been in their interactions with the soil microflora (the "catalytic" effect of Macfadyen, 1961). Most recently these interactions have been viewed in relation to nutrient elemment cycling. While microarthropod bodies have been implicated as potentially important sinks and sources of nutrients (Crossley, 1977; Luxton, 1979; Wallwork, 1983), their low standing crops make the amount insignificant in relation to quantities immobilized by microorganisms, particularly fungi (Seastedt, 1984). The principal significance of mycophagous mites seems to lie in their ability to extract limiting nutrients (*e.g.,*

nitrogen) from fungal standing crop and, with their death or excrement, make them available for rapid reuse in further mycelial or bacterial growth, with concomitant organic substrate decomposition (Whitford and Santos, 1980; Seastedt, 1984). As with comminution, the impact of soil mites will be some function of the amount of fungal tissue consumed. Estimates are rare, but consumption may be quite low in relation to fungal standing crop (Mitchell and Parkinson, 1976). The relationship of soil mites and other microarthropods to nutrient dynamics is complex (Seastedt, 1984) and whether their feeding helps fungal growth, or suppresses it and shunts decomposition to bacterial pathways (which may be more rapid and complete), depends on characteristics of the site, the substrate, and the organisms involved.

Considering their high densities, taxonomic diversity, conservative population dynamics, and a broad mix of specialized and opportunistic feeding habits, oribatid mites seem to be stable background decomposers, analogous in a way to most predaceous arachnids in that they seem incapable of rapidly adjusting to changes in resource availability. Crossley (1977) has contrasted this K-strategy to the r-strategy of collembolans, which may dominate microbial feeding at times of rapid growth; the r-strategy may also characterize fungivorous Prostigmata.

To better understand these processes we need more detailed information on feeding specificities of caprophagous and mycophagous mites, not just what will be eaten, but the physical and chemical cues which provoke feeding (Cancela de Fonseca and Poinsot-Balaguer, 1983). We also need comparative information, from a wide vaiety of habitats, on the portion of organic matter input comminuted by oribatid mites and similar estimates on consumption of microbial standing crops by mycophagous mites. Comparative studies of longevity of fecal pellets and the extent and role of their bacterial enhancement in subsequent decomposition will also be important.

Some Additional Areas Needing Attention

Many other aspects of the biology and ecology of saprophagous and mycophagous soil mites are in need of continued study, and these can be used to illustrate or test many current general hypotheses. Biotic and abiotic determinants of community structure and microdistribution are known only in very general terms (see Anderson, 1975; Usher *et al.*, 1982; Wallwork, 1983). The importance of competition in determining coexistence of similar saprophagous and mycophagous mites (*e.g.,* Anderson, 1978) is an especially timely subject. Are the consistent size differences observed between coexisting pairs or series of congeneric oribatid mites (Walter and Norton, in press) due to limiting similarities imposed by exploitation competition (if so, what is the resource?), or are they simply manifestations of reproductive isolation mechanisms? Much remains to be learned about the distribution and biology of deep-soil mites, especially the Prostigmata (Kethley, in press). Gerson (1983) has recently suggested that filtrates from surface organic substrates may be an important resource for such animals.

Inter- and intra-habitat dispersal is another aspect which is virtually unstudied. We have some knowledge of dispersal in species restricted to specialized, insular microhabitats (*e.g.,* Binns, 1982; Norton, 1980), but knowledge of the potential for colonization (and redistribution within habitats), is important, especially in studies of perturbation effects. The use of soil arthropods as indicators of soil conditions and disturbances is in its infancy (Lebrun, 1979) but suffers from the paradox that many responses are species-specific, yet the diversity and inadequate state of taxonomy for most groups (see below) makes identification extremely difficult, even for "experts." The list of necessary reseach in biology is long, and the challenges are many, even without entering more basic areas of physiology, functional morphology and

genetics.

SYSTEMATICS

As has been echoed many times by ecologists and systematists alike, sound systematics is prerequisite to sound biology and ecology (*e.g.,* Wilson, 1971). This does not simply mean having good species descriptions and monographs available. Well-corroborated hypotheses on patterns of evolution (phylogenies) are essential in attempting to put biological attributes and problems in an evolutionary perspective. That this "echo" has most often fallen on deaf ears can be easily seen in the fact that despite the ubiquity and diversity of saprophagous and mycophagous soil mites, in all of North America a single research position is devoted to study of their systematics (Dr. V. Behan-Pelletier, B.R.I., Ottawa).

As with the biological section, I deal here primarily with those soil arachnids of most interest with regard to soil structure and fertility, and make no attempt to summarize knowledge of major predaceous groups. Edaphic members of Mesostigmata represent about 120 genera in 30 families (Krantz and Ainscough, in press). Currently no North American monographic works, comparable to the European works of Karg (1971) or Ghilyarov and Bregetova (1977), are available. However, a valuable contribution has been made recently by Krantz and Ainscough (in press), who provides generic keys and references. Dondale (in press), Edgar (in press) and Muchmore (in press) have provided keys and guides to the literature for soil spiders, harvestmen, and pseudoscorpions, respectively. Of particular importance is the fact that the long-neglected erigonine linyphiid spiders (Micryphantidae) which are abundant and diverse in soil litter, are currently receiving attention (*e.g.,* Millidge, 1983).

Saprophagous and Mycophagous Soil Mites: Descriptive Taxonomy and Monographs

Kethley (in press) has provided a family key and comprehensive reference list for soil Prostigmata, but no North American monographs comparable to those for the Palearctic fauna (*e.g.,* Schweizer and Bader, 1963; Ghilyarov, 1978) currently exist, although a few families are known in some detail, at least at the generic level. Many species-level determinations even in common mycophagous groups such as Eupodidae, Pygmephoridae, Scutacaridae, Tarsonemidae, and Tydeidae are impossible. Of the approximately 14,000 described species of Prostigmata in the world, Kethley (in press, and 1982) suggested that nearly 6,400 (678 genera in 57 families) are associated in some way with the soil/litter community, and that less than 100 are mycophages. For those familiar with the true diversity of the aforementioned families in soils, it is obvious we have a long, long way to go in descriptive taxonomy.

Oribatid mites are perhaps the most successful of all soil arthropods (Johnston, 1982). The approximately 6,500 known species-group taxa represent more than 1,000 genera in about 150 families. As in most other mite suborders, the known species constitute a small fraction of the extant number. For this group also, there are no monographs for the North American fauna, or any substantial part of it. In contrast, monographic works on the Palearctic fauna steadily appear (*e.g.,* Sellnick, 1928, 1960; Willmann, 1931; Bulanova-Zachvatkina, 1967; Kunst, 1971; Ghilyarov and Krivolutsky,1975; Suzuki, 1978; Niedbala, 1980; Balogh and Mahunka, 1983). Whereas careful use of these works can be helpful in identifying the nearctic oribatid mite fauna, special care must be used in assigning species names. The North American literature is replete with wrongly applied names of European species. Especially helpful have been the several generic-level world or holarctic monographs of Balogh (*e.g.,* 1965, 1972), but the

inadequate state of knowledge of the Nearctic fauna makes the distributional information in these works misleading. Also, generic concepts in many families, developed primarily in Europe, are not applicable to the North American fauna.

Ever since their serious initiation at the turn of the last century, in the works of Nathan Banks, descriptive studies on North American oribatid mites have been the domain of only one or two productive researchers, and the quality of work has varied tremendously. All of this will be referenced in a catalogue of oribatid mites of Canada and the continental U.S., which is nearing completion by Drs. V.G. Marshall, R.M. Reeves and me. It lists approximately 1,000 species-group taxa and will be especially important as a guide to the literature. It does not substitute for much-needed monographs, however, and as in other soil mite groups, the taxonomy of North American oribatid mites is not yet "user-friendly."

One problem with most mite monographs is that they do not deal with immatures. Whereas in most Mesostigmata and many Prostigmata the immatures and adults are easy to associate, this is not so for the brachypyline, or "higher" oribatid mites, which are the most abundant and diverse groups in most soil extracts. If extractions are efficient, immatures are obtained in high numbers and much information is lost by lumping them as "oribatid nymphs." The only key available for immatures is that of Wallwork (1969), and this is necessarily very general and incomplete. Although the importance of immatures in systematics and ecology has been stressed (*e.g.,* Grandjean, 1953; Trave, 1964) relatively few researchers make the effort to describe them.

Supraspecific Classification and Phylogeny

Before concluding, a few statements should be made about trends in the classification of soil arachnids, and the general philosophical issues behind them. Historically, most classifications have been based on *differences* between groups of organisms and little distinction was made between classification and identification, which should be quite opposite procedures. Classifications have tended to be pragmatic mirrors of identification keys, but the price paid for such a simple translation is loss of the evolutionary perspective. Like keys, classifications based on differences, tell us nothing about evolutionary relationships, which can only be deduced from patterns of *similarities* between groups. As an example, let us examine the recent classification of enarthronote oribatid mites by Balogh and Mahunka (1983) (their Arthronota). Two cohorts are recognized within this group, the Euarthronota and Arthroptyctima. The first has nine superfamilies, all with a single family. The families are so separated because of discrete morphological differences. The Arthroptyctima has two superfamilies, each with a single family. While this classification could readily be translated into a key, it carries essentially no evolutionary information. The Arthroptyctima is biphyletic; the character on which the grouping is based (ptychoidy) is clearly derived by convergence so that the closest relatives of each of the two superfamilies are not each other, but are in different superfamilies of Euarthronota (see Norton *et al.,* 1983; Norton, 1984). Also, even though there is much to be learned about relationships in the families constituting Balogh and Mahunka's Euarthronota, some relationships are easily defined (Norton *et al.,* 1983; Norton, 1984) yet completely masked by their excessively split, redundant classification. Scientists who are seeking an evolutionary understanding of biological processes, such as the distribution of feeding strategies and their effects on soil structure and fertility, or adaptations to desert conditions, or whatever, are thus done a disservice.
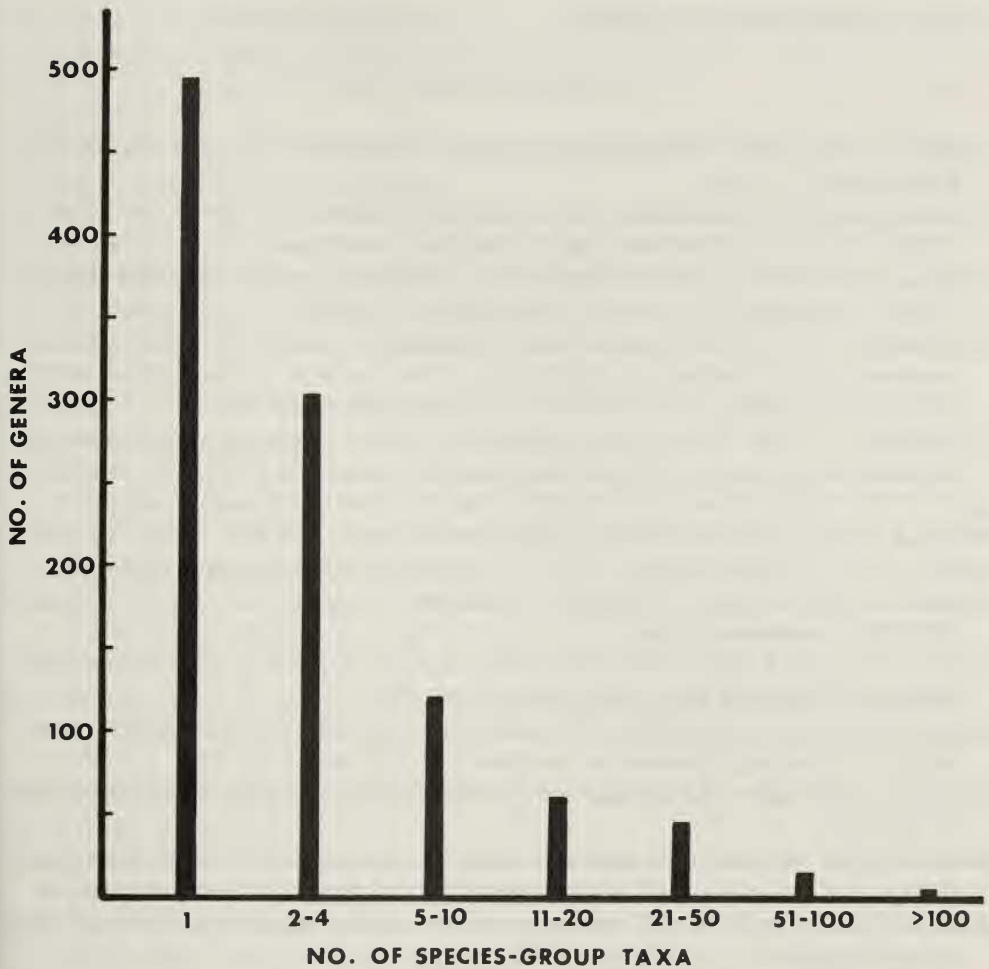
Fig. 1. Present distribution of species-group taxa among genera of oribatid mites (worldwide).

The effects of emphasizing differences can also be seen in the distribution of species and subspecies among genera (Fig. 1). Almost half (47%) of the approximately 1,000 proposed oribatid mite genera are monotypic and three-quarters have fewer than five species-group taxa. The trend is also growing; in 1980, the monotypic genera constituted 43% of the total. Clearly the reason is an emphasis on differences for purposes of identification and results in the same loss of evolutionary information.

Classifications based on similarities, in particular similarities which are evolutionary "novelties," are becoming more popular. Such classifications require more thought and effort. They are based on the development of testable hypotheses of evolutionary patterns, or phylogenies, the techniques for which are grouped under the rubric "cladistics" or "phylogenetic systematics" (see Wiley, 1981). It is not always possible or even necessary to develop phylogenies when doing descriptive work, but the principle of "classification by

similarity" can be adhered to, nonetheless.

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